

Sexual selection for novel partners: a mechanism for accelerated morphological evolution in the birds-of-paradise (Paradisaeidae)

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In morphological form and behavioural display, the 40–45 species of birds-of-paradise (Paradisaeidae) currently recognized (Mayr 1962, Sibley & Monroe 1990) are one of the most spectacular and diverse families of passerines. Recent molecular studies indicate that this diversity has arisen rapidly. Thus in a protein allozyme study, Christidis & Schodde (1992) found genetic distances (Nei 1978) ranging from only 0.09 to 0.37 among six morphologically distinct genera of paradisaeine birds-of-paradise. Using the avian protein molecular clock of Marten & Johnson (1986), the following dates of divergence can be estimated for the genera examined by Christidis & Schodde (1992). The manucodes (*Manucodia*) and the paradisaeine lineage of polygynous species split from one another 7 million years ago, the riflebirds (*Ptiloris*) from the core polygynous clade 4 million years ago, and then the remaining genera examined—*Cicinnurus*, *Epimachus*, *Parotia* and *Lophorina*—from one another within the last 2 million years. These dates are proportional to, though considerably less than, those calibrated from DNA-DNA hybridization by Sibley & Ahlquist (1985). According to their data, manucodes diverged from other paradisaeines some 18 million years ago, and most polygynous genera from one another within the last 4 or 5 million years. Irrespective of the accuracy of these estimates, it seems clear that the polygynous New Guinean birds-of-paradise exploded into their present array of forms recently. Palaeogeographic events match the protein data in particular. The massive cordilleras in which the New Guinean radiation in paradisaeines is centred today were raised only 2 to 3 million years ago, after connections with ancestral stocks of Australian-centred *Ptiloris* would have been sundered (Doutch 1972, Dow & Sukatmo 1984).

What factors can account for such a rapid rate of morphological change? Two which have been proposed are sexual selection (Darwin 1871) and niche shifts (Diamond 1986). Diamond (1986) has compared the diversification in birds-of-paradise to radiations in other Pacific island passerines, the Hawaiian honeycreepers (Drepanididae) and Darwin's finches (Geospizinae). Diversification in these groups is believed to have been driven by exploitation of suites of niches unoccupied by other birds. Such circumstances, however, do not apply to the birds-of-paradise which, in contrast, have evolved *in situ* within the continental Australo-Papuan avifauna, alongside pigeons, orioles (Oriolidae) and the larger honeyeaters (Meliphagidae) which use the same range of niches: arboreal frugivory and insectivory. Shifts in

environmental selection for natural variants are also unlikely to explain paradisaeine diversity because individual variation within populations is no greater than in other species of birds (Diamond 1986).

If sexual selection is the principal force that has driven morphological divergence within the birds-of-paradise, what is its underlying mechanism? Diamond (1991:176) has suggested that the 'handicap model' of Zahavi (1975) may operate in birds-of-paradise. According to this controversial hypothesis, secondary sexual characteristics may in fact operate to reduce the ecological fitness of their carriers. Furthermore, characters such as bright and conspicuous plumage serve to highlight to the opposite sex the underlying competence of any individual capable of flourishing despite such disability.

Another possible mechanism is the 'runaway' selection hypothesis proposed by Fisher (1930). According to this model, a female inherits genes from her male parent that predispose her to prefer a particular trait in males—long gaudy tail feathers for example. Males with gaudy tail feathers pass genes continuously to their daughters that compel them to choose males with ever gaudier tail feathers, accelerating a cycle of 'runaway' evolution. In support of this model, Andersson (1982) found that female Long-tailed Widowbirds *Euplectes progne* preferentially chose males that had had their tails artificially lengthened.

One consequence shared by both 'handicap' and 'runaway' selection models is the accentuation, through sexual selection, of variation already present in the population. Thus constrained, these mechanisms do not seem to explain either the range or rapidity of morphological evolution in polygynous paradisaeine birds-of-paradise. Instead, we postulate that preference by females for a mate that is novel or unique provides the answer.

Ten Cate & Bateson (1988) have suggested that preference for conspicuous and slightly novel partners may evolve in some instances to avoid inbreeding. This is usually offset by imprinting, through which mate preference is affected by learning the appearance of the opposite sex from parents. In polygynous species, however, males do not tend the young and so female chicks have no male model on which to imprint. Male chicks may learn the form of the mother, but, as is well-known (Diamond 1972), female paradisaeines are mostly similar in plumage and unlike the diversely plumaged males. Such a situation, in which females, unconstrained by early imprinting, are attracted to novel males, could lead to a cycle driven by preferences for gross mutations. Female selection for novelty in this form may in turn compensate for any initial ecological or physiological disadvantage produced by major mutations. Because of breeding structure, furthermore, effective population size will be lower in polygamous than monogamous species. Therefore, any mutation or hybrid trait conferring such a selective advantage should become fixed rapidly in polygamous species.

Such a mechanism may also account for the occurrence of sporadic inter-generic hybridization in birds-of-paradise (summarized in Table 1). In those species of birds-of-paradise where mating behaviour has

TABLE 1

Hybridization recorded between genera of birds-of-paradise (from Stresemann 1930, Mayr 1962, Gray 1958, Fuller 1979). Key: +=hybrids recorded, P=polygynous, ?=no data, A=allopatric, A?=possibly some contact in range

	Mating system	1	2	3	4	5	6	7	8	9
1 <i>Astrapia</i>	P	***								
2 <i>Epimachus</i>	P	+	***							
3 <i>Lophorina</i>	P		+	***						
4 <i>Parotia</i>	P			+	***					
5 <i>Cicinnurus</i>	P	A		+		***				
6 <i>Paradisaea</i>	P				+	+	***			
7 <i>Paradigalla</i>	?		+	+	+	A	A?	***		
8 <i>Seleucidis</i>	P	A	A?	A	A		+	A	***	
9 <i>Ptiloris</i>	P	A		+	A?		+	A	+	***
10 <i>Pteridophora</i>	P			A	A?	A	A		A	A

been studied in detail, it appears that females actively choose males on the basis of display and plumage characters to maximize 'fitness' of their offspring (e.g. Pruett-Jones & Pruett-Jones 1990). In such species, interspecific hybridization should be eschewed. In paradisaeines, nevertheless, hybridization not just between species but even 'genera' does occur (Table 1). In that table, *Paradisaea* × *Parotia* is newly recorded, represented by an individual *Paradisaea rudolphi* × *Parotia lawesii* in feminine plumage from Baiyer River, Papua New Guinea, in the Australian Museum (AM 0.40100); it has the ventral markings and dusky bill of *Parotia lawesii* and the all black head, white orbital marks and heavy decurving bill of *Paradisaea rudolphi*. From Table 1, it is evident that hybrids have been recorded between most polygynous genera that are sympatric. Because natural hybridization in other avian families invariably involves species that resemble one another (Gray 1958), some of these crosses, as between *Astrapia* and *Epimachus* and between *Lophorina* and *Cicinnurus*, are extraordinary, so different are the parental taxa in morphology and plumage patterns. Under the mechanism of sexual selection proposed here for birds-of-paradise, preference for novel or unique males would account for such inter-generic hybridization.

According to this interpretation, female choice in birds-of-paradise differs from the 'relative choice' model of Lande (1981) and Zuk *et al.* (1990), which has females comparing males to select those with the most exaggerated form of secondary sexual characters, irrespective of the nature and frequency of the trait. In our model, female choice is directed towards the male with the most unique or different form of secondary sexual character. It is a model that can be tested by simple experimentation in the field. For example, the plumes of selected males could be altered in colour and shape, and mating success recorded before and after modification. Traits could be altered either to accentuate present variation (*cf.* Andersson 1982), or to appear as new.

Species such as those of *Paradisaea*, which congregate conspicuously at display trees, would be ideal for such investigation, particularly as they form hierarchies in dominance (Beehler 1989) which could be changed by modifying the plumage of individual males. According to the mechanism canvassed here, we predict that mating success will increase significantly in those males altered most radically from the norm.

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